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FACTORS INFLUENCING FLOWER SIZE IN NICOTIANA WITH SPECIAL REFERENCE TO QUESTIONS OF INHERITANCE[1]

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I. Introduction

During the past five years the inheritance of flower size has been of interest in connection with the study of hybrids made in the University of California Botanical Garden between various pure lines of Nicotiana species and varieties. Three flower size varieties of *N. acuminata* (Graham) Hook. (Setchell, 1912, p. 23) were crossed back and forth and the hybrids examined up to and including F_3 (cf. Goodspeed, 1912 and 1913, (1)); species hybrids between *N. sylvestris* Speg. & Comes (Setchell, loc. cit., p. 29) and a number of *N. Tabacum* L. varieties (ibid., pp. 3–11) have also been under observation and their F_1 flower size and the size of the flowers in the case of crosses of the parents back onto the hybrids have been studied in detail. At the present time a study is being made of the flower size of a self-fertile hybrid between *N. Langsdorfii* Weinm. and *N. Langsdorfii* var. *grandiflora* Comes (Setchell, 1912, p. 15) which should be of interest because of the marked difference in flower size of the parental types.

In the collection of some 25,000 measurements on the length of corolla tube and the spread of corolla limb of flowers on the various hybrids above noted certain very definite difficulties have been encountered. These difficulties have had their influence as well in determining the technique of taking the measurements as in directly influencing the value and interpretation of the general results obtained. East (1913, pp. 177 and 178) finds reason to believe that corolla size, which he recognizes as a "character complex," is "comparatively constant under all conditions attending development." In this connection he refers to the well-known fact that other size characters, in contrast to this comparative stability of corolla size, are subject to a

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rather greater degree of fluctuating variability under similar conditions attending development. Thus we read that, "During the past four years I have grown about 20 species of Nicotiana in considerable numbers. They have been grown under very diverse conditions. Some have been starved in four-inch pots, others have had the best of greenhouse treatment; some have had poor field conditions, others have had all field conditions practically at their best. The height of the plants, the size of the leaves, and similar size complexes have varied enormously, but the size of the corollas has varied scarcely at all. For example, plants of *N. sylvestris* Speg. & Comes grown to maturity in four-inch pots produced no leaves longer than 7 inches. On the other hand sister plants of the same pure line produced leaves 30 inches long in the field. Both series, however, produced flowers with the same length and spread of corolla. Furthermore, cuttings from 20 of the field plants reported in this study were rooted and grown in small pots in the greenhouse. Their blossoms were the same size as those of the field plants from which they came." The data herein to be listed seem, in our opinion, to demonstrate that in the Nicotiana cultures grown in the University of California Botanical Garden a rather different condition of affairs prevails so far as the "character complex," corolla size, is concerned. East also finds (ibid., p. 181) that in general "corolla spread is . . . correlated with corolla length." As a broad generalization this statement is undoubtedly correct. On the other hand, the fact that in our experience corolla length and corolla spread behave in a different manner with reference to their stability under "the conditions attending development," suggests that the assumption of a too definite correlation when attempting to interpret the results of studies of flower size inheritance in Nicotiana must be very guardedly indulged in. The fact that in our experience corolla size does vary distinctly under some of the most normal and inherent conditions attending development and that corolla spread and corolla length do not respond alike in this respect has in a great measure been the cause of the difficulties in technique and interpretation above mentioned.

The data presented in this report were collected in connection with a number of separate and distinct experiments, and pertinent data upon an almost equal number of plants were also available. It is the purpose of the present report to illustrate by the presentation of the results, actually accumulated in the field, the effects of various environmental and especially developmental factors in determining the expression of the "corolla complex" in Nicotiana. The extent of the data and the nature of the conclusions derived therefrom make it seem possible to establish tentative criteria in keeping with which flower size investigations, in Nicotiana at least, should be carried on and interpreted. In the present report no effort will be made to illustrate or to discuss specifically the nature or manner of the inheritance of flower size in Nicotiana. Further reports in preparation aim to take up this question in detail and to discuss it on the basis of the various considerations herein to be emphasized.

II. Experimental Material

The data presented herewith have to do with measurements on the size of flowers produced by:

1. *N. Tabacum* var. *macrophylla* Comes (Setchell, loc. cit. p. 8) in the growing season 1913. This *N. Tabacum* variety has been grown here for 6 years in the pure line and will be referred to under its University of California Botanical Garden number, U. C. B. G. 22/07.

2. The F_1 hybrid *N. Tabacum* var. *macrophylla* (22/07) ♀ × *N. sylvestris* (ibid., p. 29) ♂ which will be referred to as F_1 H_{38}. This cross was made by Professor W. A. Setchell in 1911 and the flowers on 25 F_1 hybrid plants were first measured in 1912. These F_1 plants were cut back early in 1913 and came into full flower during May of the same year. Their flowers were measured in large numbers. A second sowing of the seed of the original cross was made in 1913 and the flowers on 10 plants were measured that season. We have thus data upon the flower size of: 12 F_1 H_{38}, plants from the first sowing of the hybrid seed; 13 F_1 H_{38}, plants of 12 F_1 H_{38} coming up on their own roots; 13 (11) F_1 H_{38}, plants from a second sowing of the original hybrid seed.

Thus plant No. 1 of 13 F_1 H_{38} is plant No. 1 of 12 F_1 H_{38} growing the second year on its own roots, while plant No. 1 of 13 (11) F_1 H_{38} cannot be compared directly with any plant of 12 F_1 H_{38} or 13 F_1 H_{38}, although it is genetically of exactly the same constitution.

3. F_1 H_{137}, which is the reciprocal of F_1 H_{38}. This cross was made in 1912 and flowers on F_1 plants were measured in 1913.

4. The F_1 hybrid produced by crossing F_1 of the hybrid *N. Tabacum* "Maryland" (ibid., p. 5) ♀ × *N. Tabacum* "Cavala" ♂ with *N. sylvestris*. The garden number of this cross is H_{44}. It was made in

1911 by Professor Setchell and F_1 flowers were measured in 1912. These plants, also, were cut back early in 1913 and were fully in flower during May of the same year. Cuttings of certain of the F_1 H_{44} plants were rooted in the greenhouse during the fall and flowered under glass in the early spring. Another sowing of H_{44} was made in 1913 but no measurements were taken upon the flowers of these plants.

The technique of taking the measurements on spread or diameter of corolla limb was the same as that used in the previous studies on the inheritance of flower size in Nicotiana (cf. Goodspeed, 1912, p. 138). The measurements of spread of corolla limb herein listed were taken without the use of any holder and with the corolla limb supported between the thumb and forefinger. Length of corolla tube was taken to be the distance from the point of union of calyx and pedicel to the point where the under side of the reflexed limb joins the corolla tube. In the case of species of Nicotiana here dealt with the flowers were fully open throughout the day as contrasted with the more or less vespertine *N. acuminata* varieties and their hybrids, which were studied previously.

III. Factors Influencing Flower Size

1. *"Age of Plant" Factor*

The heading "'Age of Plant' Factor" has to do with the fact that a tobacco plant during the first few days after coming into flower bears flowers which differ in size from the flowers which it bears later in the growing season normal for this particular species or variety. It also serves as a heading for the discussion of the fact that the flowers borne on plants cut back and growing on their own roots a second season differ in size from the flowers borne on the same plants the first year. The following tables (Tables I to V) are intended to illustrate the situation with reference to early and late flowering on the same plant. These are condensed statements of the full records and have to do with the frequency distributions for the entire population in each case. On account of their extent it would hardly be possible to include the complete records for each plant on the different dates on which the flowers were measured.

In the tables the plants are arranged according to the mean flower size of the particular date or period in question. The mean flower size in every case for each date was calculated and also a mean for the period during which the measurements were taken. This last is the mean designated under "means for totals" in the tables. It was calculated simply by taking the average flower size of all the flowers measured during the entire period. On account of the different numbers of flowers measured on the different dates, this calculation would differ somewhat from a mean based on equal weighting of each date, but such a procedure does not appear to have any particular advantage for the purposes of this discussion.

TABLE I*a*

Frequency Distributions for Spread of Corolla in U. C. B. G. $13^{22}/_{07}$,

Designation	Class Centers in Millimeters														No.	Mean	Coef. Var.
	19	20	21	22	23	24	25	26	27	28	29	30	31	32			
Means for totals..........							7	25	28	7	6	1	1		75	26.83±.09	4.45±.24
Means for first dates......							1		13	25	25	8	1	2	75	28.48±.09	4.11±.23
Means for last dates.......	1	3	8	11	15	5	10	10	1	3	3	3	2		75	24.19±.22	11.59±.64
Means for different dates ..		1	2	4	6	2	6	6	12	18	12	4		2	75	26.69±.20	9.77±.54

Tables I*a* and I*b* give the frequency distributions for spread and length of corolla, respectively, of 13 22/07 under designations which are in part at least self-explanatory. For example the line in Table I*a* designated "means for totals" gives the distribution of the means of the 75 plants under consideration for the entire number of measurements taken. Thus for Plant No. 1 of 13 22/07, 28.73 mm. represents the mean size of corolla spread as determined from the measurements of flowers on seven different dates from July 28 to September 22, and including a few flowers late in the season from the terminal inflorescence. In a few cases some open flowers not yet shedding pollen have been included in these calculations. An average of about 40 flowers per plant was measured during this period, not more than 80 nor less than 25 on any one plant. The "means for first dates" simply gives the distribution of means calculated from the flowers measured on the first date and likewise the "means for last dates" gives the distribution of means calculated from the flower measurements on the last date. The distribution designated "means for different dates" is one such as might be obtained if a large number of plants were measured, each on a single date; *i. e.*, if a worker began measuring the flowers on his plants at a certain date and gradually worked through the lot during a period corresponding to the one considered here. This distribution was obtained in this particular instance by grouping the means for the first 25 plants on the first dates, the second 25 on a mid-date, and the third 25 on the last date together in one distribution. Table I*b* has to do with corolla tube length of the same plants, and the same explanations of course apply to it.

TABLE I*b*

Frequency Distributions for Length of Corollas in U. C. B. G. $13^{22}/_{07}$,

Designation	Class Centers in Millimeters											No.	Mean	Coef. Var.
	38	39	40	41	42	43	44	45	46	47	48			
Means for totals.....				1	3	6	34	28	2	1		75	44.27±.07	2.13±.12
Means for first dates .						1	5	29	29	10	1	75	45.60±.07	1.96±.11
Means for last dates .	2	2	10	17	9	15	8	10	1	1		75	42.25±.15	4.58±.25
Means for different dates............	2	1	5	6	4	7	8	24	13	3	2	75	43.96±.18	5.18±.29

The period during which measurements were taken was from July 28 to August 30, although a few of the plants were measured again on September 22. Measurements of flowers borne among the developing seed capsules on the terminal inflorescence and also of open flowers which had not yet begun to shed pollen, when such were taken, were separately designated in the records. These classes of flowers show significant differences in flower size, as will be shown later on in this paper, and a haphazard selection of the flowers to be measured might easily give undue prominence to some one of these classes. They were not however excluded in the calculation of the total mean for each plant, but the error introduced in this manner is very slight on account of the small number measured in proportion to those fully open and borne on the later flowering laterals.

Certain difficulties and in some cases the arbitrary nature of the groupings are quite evident. As has been noted the measurements were taken in connection with a number of separate experiments and obviously the dates chosen for making the measurements were dictated by convenience rather than with the present use of the data in mind. The reason for the groupings will be explained in the pages that follow and the fact that, notwithstanding the above situation, the data bring out the facts to which we desire to call attention is sufficient justification for any slight discrepancies which may be apparent.

Table I*a* brings out the fact that the mean spread of corolla limb in the case of the means for 75 plants of *N. Tabacum* var. *macrophylla* (U. C. B. G. 22/07) is 26.83 ± .09 mm., and the range of fluctuation is 7 mm., from 25 to 31 mm. On the other hand, the total range in corolla spread as shown by the complete records amounted to 18 mm., from 18 to 35 mm.; and for individual plants as high as 14 mm. Similarly for length of corolla tube, as shown in Table I*b*, the mean was 44.27 ± .07 mm. with a range of fluctuation of 7 mm., from 41 to 47 mm. The complete records, again, show a total range of 18 mm., from 33 to 50 mm., for length of corolla tube. These facts are based upon measurements continued for nearly one month or in a few cases for over one month of the blooming period normal for this species and variety. If now the mean flower size is determined on the basis of measurements taken during the first 3 or 4 days of this period, the mean spread of corolla is 28.48 ± .09 mm., as contrasted with 26.83 ± .09 mm., and the length of corolla is 45.60 ± .07 mm. as contrasted with 44.27 ± .07 mm. Similarly if the mean is determined by measurements taken on all the plants at the end of this period, the mean corolla spread is 24.19 ± .22 mm. as compared with the mean for totals of 26.83 ± .09 mm. and the mean for the first dates of 28.48 ± .09 mm. In the same way for the length of corolla we have a mean of 42.25 ± .15 mm. at the end of the season, while the mean for totals is 44.27 ± .07 mm., and the mean at the beginning of the season is 45.60 ± .07 mm. If in the third place the mean is derived by measuring flowers on the first third of the plants early in the season, on the second third in the middle of the flowering season, and on the remainder of the plants toward the end of the season, we have for spread a mean of 26.69 ± .20 mm. which, as would be expected, is practically the same as the mean for totals 26.83 ± .09 mm., but differs from the means for the first and last dates which are 28.48 ± .09 mm. and 24.19 ± .22 mm., respectively. Similarly with reference to length of corolla we have a mean of 43.96 ± .18 mm. for such a distribution which is very close to the mean for totals of 44.27 ± .07 mm., but is distinct from the means of the first or last dates which are 45.60 ± .07 mm. and 42.25 ± .15 mm., respectively. The amount of these differences and their probable errors are tabulated in Table 6, where they may be compared with similar differences shown in other series of plants.

The differences between the means according to different times of measurement and different modes of arrangement furnish the basis for the more significant differences in variability under these same conditions. Thus we see that although the mean for "different dates," 26.69 ± .20 mm., does not differ sensibly from the "mean for totals" of 26.83 ± .09 mm., yet the coefficient of variability for the former distribution is over twice as great as in the latter case. The difference between the two is 5.32 ± .59 per cent, which is certainly large enough in comparison with its probable error to acquire considerable significance. The proportionate increase in variability for the corresponding length arrays is very slightly higher than that for width arrays, but for all practical purposes the same. Here again the difference between the two coefficients of variability, 3.05 ± .28 per cent is large enough to be of unquestionable significance. In figures 1 and 2 are given a graphic representation of the facts brought out in these tables.

It seems fair to assume that to determine the constants for flower size of a large series of plants, an F_2 population for example, the flowers on the plants would naturally be measured either all of them during the beginning of the flowering season, all toward the end of the season, or most probably in some such fashion as is expressed in the distribution of "different dates." Peculiarly enough published reports give us no account of the way in which the measurements of flower size were collected. It seems fair, however, to assume that in field work measurements of 25 flowers should represent the minimum required to give even an approximately fair mean flower size for a given plant. On this basis to any one familiar with the taking of such measurements the number of operations necessary to obtain the mean distribution of flower size in a representative F_2 population represents a stupendous amount of time. With anything like the normal amount of assistance available it hardly seems possible that any such number of measurements could be accumulated in less than a month and a half; and, if so, some of the plants would be measured at the beginning, others at the middle, and still others at the end of the period of flowering. Such a system would merely give a representative mean and would not give a body of data suitable for the calculation of other constants. The only other alternative involves the measuring of a few flowers on each plant during the first week of the season and repeating this process each week throughout the season. Even this, however, would involve the necessity of taking a larger number of measurements than is ordinarily possible during such a time. We feel that a distribution based upon means derived from measurements taken throughout the growing and flowering season is, with one possible exception to be noted in the following pages, the only representative distribution. Such a distribution expresses the entire demonstrable series of developmental changes in the flower which accompanies the normal ontogenetic plant processes. It is hardly necessary to point out the bearing which results such as these have on the interpretation of the inheritance of similar characters based on a comparison of constants derived from small parental and F_1 populations with very large F_2 populations. The fact that is decidedly significant in connection with the study of the inheritance of flower size is that the distributions of means when different parts of the total population are measured at different times is so strikingly different from the truly representative distribution derived from the measurement of all the plants throughout the whole season.

In Tables II to V we are concerned with the flower size of three of the semi-sterile hybrids of *N. Tabacum* varieties and *N. sylvestris* which have been mentioned in previous communications (cf. Goodspeed, 1913, 2). Tables II*a* and II*b* have to do with the means of spread and length of flowers on the plants of F_1 H_{137}. The facts brought out in these tables emphasize those already demonstrated by

TABLE II*a*

Frequency Distributions for Spread of Corollas in 13 F_1 H_{137}

Designation	Class Centers in Millimeters										No.	Mean	Coef. Var.
	30	31	32	33	34	35	36	37	38	39			
Means for totals...........					1	4	4				9	35.33±.15	1.89±.30
Means for first dates.......									6	3	9	38.33±.11	1.23±.20
Means for mid dates........				1	1		1	3	1	2	9	36.67±.44	5.30±.84
Means for last dates........	1	4	2	1	1						9	31.67±.26	3.65±.58

TABLE II*b*

Frequency Distributions for Length of Corolla in 13 F_1 H_{137}

Designation	Class Centers in Millimeters							No.	Mean	Coef. Var.
	51	52	53	54	55	56	57			
Means for totals...........				1	4	4		9	55.33±.11	1.21±.19
Means for first dates........						7	2	9	56.22±.09	.74±.12
Means for mid dates........				3	3	3		9	55.00±.18	1.49±.24
Means for last dates........	1		4	3		1		9	53.44±.28	2.36±.37

Tables I*a* and I*b*. For spread of corolla, the range shown in the distribution designated "means for totals" is only 3 mm., from 34 to 36 mm. The range of fluctuation of flowers was 17 mm., from 26 to 42 mm. and an average of about 70 flowers was measured on each plant during a period of less than six weeks from August 9 to September 19. The difference between the spread of flowers on plants at the beginning of the flowering season, at the middle of the season, and towards its end is very striking. The results show a decrease in size from 38.33 ± .11 mm. through 36.67 ± .44 mm. to 31.67 ± .26 mm. in less than six weeks. With reference to length of corolla this progressive decrease in size is not nearly so striking, the decrease being from 56.22 ± .09 mm. through 55.00 ± .18 mm. to 53.44 ± .28 mm. The number of plants measured in this and in other cases is very small, but the fact that the measurements refer to the same plants gives them an added importance which compensates for this defect. No attempt was made to arrange the individual means into a distribution of "means for different dates"; but it is readily apparent from the data given that such an arrangement would have shown a more notable proportionate increase in the coefficient of variability than was shown in 13 22/07.

As was above noted H_{38}, the cross *N. Tabacum* var. *macrophylla* (U. C. B. G. 22/07) ♀ × *N. sylvestris* (U. C. B. G. 107/01) ♂, was made in 1911 and flowers were first measured in 1912. Tables III*a* and III*b* show the size of flowers borne by plants from a second sowing of the 1911 seed which flowered in 1913. The number of plants is again small but as explained above this fact should not detract from the significance of the data here reported. The period of measurement here was greater than in the previous cases, from August 4 to November 7, slightly over 3 months; and of the number of measurements taken,

TABLE III*a*

Frequency Distributions for Spread of Corollas in 13(11) F_1 H_{38}

Designation	Class Centers in Millimeters											No.	Mean	Coef. Var.
	31	32	33	34	35	36	37	38	39	40	41			
Means for totals				2	6	2						10	35.00±.13	1.81±.27
Means for first dates						1		2	3	2	2	10	39.10±.31	3.70±.56
Means for mid dates			2	1		2	2	2	1			10	36.10±.43	5.60±.85
Means for last dates	1	2	2	5								10	33.10±.22	3.15±.48

an average of over 80 for each plant, about half were taken on the last date of measurement. Here we have for spread the distribution

TABLE III*b*

Frequency Distributions for Length of Corolla in 13(11) F_1 H_{38}

Designation	Class Centers in Millimeters								No.	Mean	Coef. Var.
	51	52	53	54	55	56	57	58			
Means for totals.........			4	4	2				10	53.80±.16	1.39±.21
Means for first dates.....					1	2	2	5	10	57.10±.22	1.83±.28
Means for mid dates.....		1	4		3	2			10	54.10±.29	2.54±.38
Means for last dates......	3	2	2	2	1				10	52.60±.29	2.58±.39

of the "means for totals" showing a range of but 3 mm., from 34 to 36 mm.; although the range of flower size on these plants amounts to 21 mm., from 23 to 43 mm. The mean of the "means for totals" distribution is 35.00 ± .13 mm. as contrasted with 39.10 ± .31 mm. for the "first dates," 36.10 ± .43 mm. for the "mid dates," and 33.10 ± .22 mm. for the last dates. This means for the spread of corolla a progressive decrease of 6 mm. in two steps within the period of measurement. For the flowers of individual plants we have in some cases a greater decrease in mean flower size during the period. Thus in Plant 4 there is a decrease in flower size of 8.11 mm., from 40.00 to 31.89 mm., within one month, and in the distribution of means for some of the other individual plants we have nearly as great a decrease in size during the period of measurement. The measurements on length of corolla show, in a lesser degree, the same situation. Within the period of measurement, the lengths decreased 4.50 mm. and the measurements on some of the individual plants on different dates show a correspondingly larger decrease in length. Thus for Plant 4 the decrease was 6.44 mm., from 58.00 to 51.56 mm. during one month. The increase in the coefficient of variability during the period of measurement is again very marked and would obviously be still more so, if the system of arrangement of "means for different dates" followed in Tables I*a* and I*b* had been carried out.

Tables IV*a*, IV*b*, V*a*, and V*b*, have to do with two F_1 hybrids made between *N. Tabacum* varieties and *N. sylvestris.* 12 F_1 H_{38} and 13 F_1 H_{38} described in Tables IV*a* and IV*b*, do not differ genetically from 13 (11) F_1 H_{38} with which Tables III*a* and III*b* are concerned. They represent measurements on flowers of the plants from the first sowing of the H_{38} hybrid seed under the designation 1912, and on these same plants of the first sowing cut back and blooming the following year on their own roots under the 1913 designations. In 1912 the 14 or 15 flowers measured on each of the 25 plants of F_1 H_{38} were all measured on the same date late in the season, on October 31. These plants began to go out of flower during the last week of December and were cut back early in February. They soon put out new laterals which began to bear flowers early in May. In Tables IV*a* and IV*b* are given the distributions of means for spread and length of 21 of these plants. The remaining four of the original plants were lifted into pots and subsequently flowered in the greenhouse. The significance of the designation "means for totals of same plants 1912" is thus apparent. Tables V*a* and V*b* are arranged in exactly the same manner as Tables IV*a* and IV*b*. Twenty-four plants were originally measured

TABLE IV*a*

Frequency Distributions of Spread of Corolla in F_1 H_{38}

Designation	Class Centers in Millimeters												No.	Mean	Coef. Var.
	33	34	35	36	37	38	39	40	41	42	43	44			
Means for totals, 1913......		1			2	5	1	4	3	4	1		21	39.57±.32	5.49±.57
Means for totals of same plants, 1912............		2	6	8	4	1							21	35.81±.15	2.81±.29
Means for totals, 1912......		2	7	11	4	1							25	35.80±.13	2.62±.25
Means for first dates, 1913...			3		3	3	1	6	4	1			21	38.81±.31	5.43±.57
Means for mid dates, 1913..	1		1	4	1		3	2	5	3	1		21	39.05±.40	7.00±.73
Means for last dates, 1913..				1	3	2	4	2	2	3	2	2	21	40.05±.35	5.94±.62
Means for different dates, 1913..................				2	2	3	3	2	4	5			21	39.57±.30	5.09±.53

TABLE IV*b*

Frequency Distributions of Length of Corolla in F_1 H_{38}.

Designation	Class Centers in Millimeters									No.	Mean	Coef. Var.
	49	50	51	52	53	54	55	56	57			
Means for totals, 1913..........				2	2	3	10	4		21	54.57±.17	2.16±.22
Means for totals of same plants, 1912.......................			1	8	5	5	2			21	52.95±.16	2.06±.21
Means for totals, 1912...........			1	12	5	5	2			25	52.80±.14	2.00±.19
Means for first dates, 1913.......					2	2	8	8	1	21	55.19±.15	1.82±.19
Means for mid dates, 1913.......					1	2	8	7	3	21	55.43±.15	1.81±.19
Means for last dates, 1913.......	1	1		1	2	8	7	1		21	53.81±.24	3.07±.32
Means for different dates, 1913...	1			1	1	2	8	5	3	21	54.90±.26	3.27±.34

TABLE V*a*

Frequency Distributions for Spread of Corolla of F_1 H_{44}

Designation	Class Centers in Millimeters																						No.	Mean	Coef. Var.
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46			
Means for totals, 1913									2		2		1	2	1	1	4	2	3	1			19	39.42±.52	8.53± .93
Means for totals of same plants, 1912				2		2	2	1	2	4	3	1	1		1								19	33.11±.44	8.59± .94
Means for totals, 1912	1		1	3		3	2	1	2	4	3	1	1	1	1								24	32.38±.49	10.99±1.07
Means for first dates, 1913										2	2		3		2	5	5						19	38.53±.38	6.38± .70
Means for mid dates, 1913												3	1	2	2	2	3	2		3	1		19	40.16±.44	7.01± .77
Means for last dates, 1913						1		1		1	1	1		1	2	2	2	4		2		1	19	39.32±.64	10.51±1.15
Means for different dates, 1913						1		1		1		1			3	7	1			4			19	39.26±.59	9.67±1.06

in 1912, and five of them were transferred to the greenhouse when the plants were cut back. F_1 H_{38} and F_1 H_{44} were cut back on approximately the same dates.

TABLE V*b*

Frequency Distributions for Length of Corolla in F_1 H_{44}

Designation	Class Centers in Millimeters														No.	Mean	Coef. Var.
	46	47	48	49	50	51	52	53	54	55	56	57	58	59			
Means for totals, 1913....			1	1	1		2	5	1	3	5				19	53.42±.37	4.44±.49
Means for totals of same plants, 1912..........	2			2	1	1	5	1	3	2	1			1	19	52.16±.46	6.07±.66
Means for totals, 1912....	2			2	1	2	6	1	3	3	3			1	24	52.54±.42	5.84±.57
Means for first dates, 1913					1	1	2	1	4	8	1	1			19	54.05±.26	3.15±.34
Means for mid dates, 1913					1		1	4	3	2	6	2			19	54.53±.28	3.33±.36
Means for last dates, 1913	1	2			1		3	2	3	3	3	1			19	52.84±.49	5.99±.66
Means for different dates, 1913................	1	1			1		3	1	3	6	3				19	53.26±.43	5.27±.58

The 1913 measurements reported in these tables were taken with a different purpose in view and without a proper appreciation of the variation in flower size which has been shown in the previous tables. The measurements in this case were taken as the plants were just coming into flower. The method of procedure was to measure all the fully open flowers which were shedding pollen on the dates on which measurements were taken. In this way measurements were taken beginning at the first plant and working through the whole series one after the other. This process was repeated several times, the object being to obtain at least 100 measurements on each plant. As soon as this number had been exceeded on some date for some individual plant, no further measurements were taken on that particular plant during the period. Accordingly the measurements on these plants cover a rather short period from less than 3 weeks to slightly over 9 weeks, and represent a period during which the plants were coming into full flower as shown by the progressive increase in the number of flowers measured on individual plants with the advancement of the season, from as low as 4 at the beginning of the period to as high as 186 on one day at the end of the period. Naturally only a slight fluctuation in the mean would be expected during this period, particularly in view of the semi-sterile nature of the plants involved, and this is exactly the result obtained. That these plants, however, can show a wide variation in such respects is plainly evident from a comparison with the distributions for 1912.

Turning now to a consideration of these data, we find the situation somewhat different from that in the preceding tables. For the spread of corolla, the size is greater at the end of the period than at the beginning. As shown in Table IV*a* flowers on the "mid dates" of measurements are larger than on the "first dates," but smaller than on the "last dates"—there is a progressive increase in corolla spread during the period of measurement. The differences in size in both cases for the three measurements are within 2 mm. and differ from the mean of the "means for totals" by a still lesser amount. On the other hand, with reference to length of corolla in both Tables IV*b* and V*b*, the means for the first, mid, and last dates show a slight increase followed by a more marked decrease. This point will be discussed in a different connection below.

TABLE VI

Influence of the Age of the Plant on Corolla Measurements

Designation	Mean for			Difference between		
	First Date	Mid Date	Last Date	First and Mid Date	Mid and Last Date	First and Last Date
$13^{22}/_{07}$:						
spread......	28.48±.09		24.19±.22			−4.29±.24
length.......	45.60±.07		42.25±.15			−3.35±.17
13 F_1 H_{137}:						
spread......	38.33±.11	36.67±.44	31.67±.26	−1.66±.45	−5.00±.51	−6.66±.28
length.......	56.22±.09	55.00±.18	53.44±.28	−1.22±.21	−1.56±.34	−2.78±.30
13(11) F_1 H_{38}:						
spread......	39.10±.31	36.10±.43	33.10±.22	−3.00±.53	−3.00±.49	−6.00±.38
length......	57.10±.22	54.10±.29	52.60±.29	−3.00±.37	−1.50±.41	−4.50±.37
13 F_1 H_{38}:						
spread......	38.81±.31	39.05±.40	40.05±.35	+0.24±.51	+1.00±.53	+1.24±.47
length.......	55.19±.15	55.43±.15	53.81±.24	+0.24±.21	−1.62±.28	−1.38±.28
13 F_1 H_{44}:						
spread......	38.53±.38	40.16±.44	39.32±.64	+1.63±.58	− .84±.77	− .79±.74
length.......	54.05±.26	54.53±.28	52.84±.49	+0.48±.39	−1.69±.57	−1.21±.56

In Table VI the situation with reference to the differences in size of flowers borne on a plant at the beginning, toward the middle, and near the end of the flowering season or the period during which flowers were measured is summed up. This table is self-explanatory. The probable errors of all constants have been included. These differences should be significant if they are at least three times as great as their probable errors. This requirement is fulfilled in all cases except for 13 F_1 H_{38} and 13 F_1 H_{44}, an explanation for which we have suggested above.

Under the general heading "age of plant factor" the question of the differences in size of flowers on plants growing the second year on their own roots and flowers on the same plants the first year is included. On this point the data is given in Tables IV*a*, IV*b*, V*a*, and V*b*, and in condensed form in Table VII. Two facts are strikingly evidenced by the results as given. First, the spread of corolla of flowers which are produced on new vigorous laterals from plants which have been given an involuntary period of rest by cutting back is distinctly larger than the spread of flowers measured toward the end of the first season of growth and flowering. These differences are distinct and significant when compared with their probable errors. The second significant point illustrated above has to do with the relatively slight difference between the length of corolla in the case of the two periods of measurement. A difference of 6.31 ± .68 mm. in the spread of F_1 H_{44} is associated with a difference of only 1.26 ± .61 mm. in the length of the same flowers and similarly for F_1 H_{38} we have a difference of 3.76 ± .35 mm. for spread as contrasted with 1.62 ± .24 for length of corolla.

TABLE VII

Influence of Different Years on Corolla Measurements on the Same Plants

Designation	Mean		Difference
	1912	1913	
F_1 H_{38}: spread	35.81±.15	39.57±.32	3.76±.35
length	52.95±.16	54.57±.16	1.62±.24
F_1 H_{44}: spread	33.11±.44	39.42±.52	6.31±.68
length	52.16±.46	53.42±.37	1.26±.61

It must be borne in mind in this connection that the plants the first year (12 F_1 H_{38} and 12 F_1 H_{44}) were measured during the last two weeks in October or toward the end of the period of measurement as given for the other groups of plants in 1913, while in 1913 (13 F_1 H_{38} and 13 F_1 H_{44}) the flowers were measured early in their second period of blooming. In other words, if in 1913 the flowers had been measured during October, their size would undoubtedly have been more nearly equal to that given by the measurements in 1912. The dates of measurement and results as they stand are, however, particularly significant for our purpose. There is obviously, also, a decided discrepancy in the number of measurements taken in 1912 as compared

TABLE VIIIa

Frequency Distributions for Spread of Corolla of Individual Plants in F_1 H_{38},

Plant No.	Class Centers in Millimeters																										No.	Mean	Coef. Var.	M_{1913}–M_{1912}
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49				
P_1, 1912										1		1	1	3	4	2	2										14	37.50±.33	4.91±.63	
1913											4	2	4	8	23	12	12	8	13	9	2	2	1				101	39.60±.18	6.77±.32	+2.10±.38
P_2, 1912									4	1	2	1	4		2	1											15	34.87±.40	6.61±.81	
1913							2			3	4	5	16	29	31	24	21	15	11	6	5	1					173	38.57±.13	6.67±.24	+3.70±.42
P_3, 1912								1	1	1	2	2	1	2	1	3											14	35.64±.46	7.16±.91	
1913														1	3	6	18	20	23	15	8	4	2	2			102	41.71±.13	4.60±.22	+6.07±.48
P_4, 1912											2	1	4	2	3	1	1	1									15	37.00±.34	5.32±.65	
1913									3	3	11	9	23	24	42	22	23	7	4								171	37.60±.11	5.64±.21	+0.60±.36
P_5, 1912									1		3	2	2	1	5		1										15	36.20±.37	5.81±.72	
1913										3	6	5	12	27	28	19	18	15	5	8				2			148	38.49±.14	6.49±.25	+2.29±.40
P_6, 1912									2	3	3		2	3	2												15	34.93±.36	5.96±.73	
1913					2			1	5	4	1	10	8	19	17	15	21	21	26	18	15	8	3	3			197	39.85±.17	9.00±.31	+4.92±.40
P_8, 1912									2		1	2	6	2	1	1											15	35.67±.32	5.19±.64	
1913												1	4	6	7	11	16	13	13	11	14	8	5	3			112	41.38±.18	6.78±.31	+5.71±.37
P_9, 1912												1	3	1	3	3	4										15	38.07±.29	4.34±.53	
1913															3	4	6	10	17	11	13	5	5	1	1		76	42.49±.17	5.04±.28	+4.42±.34
P_{10}, 1912											2	1	6	1	5												15	36.40±.24	3.73±.46	
1913															2	1	10	10	11	4	8	6	5	4		1	62	42.71±.21	5.79±.35	+6.31±.32
P_{11}, 1912									1		4	4	2	2	1	1											15	35.40±.30	4.93±.61	
1913							2	2	1		1		2	3	5	7	20	16	12	11	4	3	3	1			93	40.46±.23	8.06±.40	+5.06±.38
P_{13}, 1912										2		6	5	2													15	35.33±.20	3.21±.40	
1913														1	4	10	10	26	12	12	6	2	3				86	42.35±.14	4.57±.23	+7.02±.24
P_{14}, 1912								2		2	3	3	3	2													15	34.47±.32	5.28±.65	
1913														1	1	8	6	17	17	24	17	7	3	1			102	42.33±.13	4.50±.21	+7.86±.35
P_{15}, 1912										1	1	2	3	2	1	2	2	1									15	37.07±.40	6.19±.76	
1913													1	2	6	5	13	10	5	5	5	1	1				54	40.72±.20	5.29±.34	+3.65±.45
P_{16}, 1912									1	1	4	6	1	2													15	34.73±.22	3.71±.46	
1913									1	1	1	1	1	6	13	13	25	20	12	9	4	3	3				113	40.29±.16	6.16±.28	+5.56±.27
P_{17}, 1912									4	2	6	2	1														15	33.60±.21	3.57±.44	
1913										1	2	2	4	6	7	11	18	19	16	18	10	4	3	3	2	1	127	41.11±.18	7.29±.31	+7.51±.28
P_{18}, 1912							2		2	3	3	3			2												15	33.73±.39	6.71±.83	
1913										1	3	9	11	11	14	20	15	14	4	1							103	38.35±.15	5.70±.27	+4.62±.42
P_{19}, 1912								1	1	2	3	1	3	2	1												15	34.73±.33	5.51±.68	
1913	2	2	1	1	2	2	1	1	2	5	6	12	7	14	11	9	11	5	2								96	36.01±.28	11.21±.55	+1.28±.43
P_{20}, 1912											2	3	3	5	2												15	36.13±.22	3.48±.43	
1913				1					1		3	8	18	17	23	7	12	3	3	6	1	5					108	38.16±.19	7.67±.35	+2.03±.29
P_{21}, 1912									1	4	3	3	1	3													15	34.53±.28	4.59±.57	
1913									1	3	2	1	1	8	6	1	1	1									25	36.56±.30	6.15±.59	+2.03±.41
P_{22}, 1912									1		2	6	1	2	2	1											15	35.67±.31	4.98±.61	
1913									1	7	6	10	10	26	11	14	13	10	5								113	37.55±.16	6.51±.29	+1.88±.35
P_{25}, 1912											1	1	5	4	1	2	1										15	36.87±.27	4.19±.52	
1913	1	1		1	3	1	2	5	3	1	5	7	4	5	8	4		1	2								54	34.48±.38	11.93±.77	−2.39±.47

TABLE VIII*b*

Frequency Distributions for Length of Corolla in Individual Plants in F_1 H_{38}

Plant No.	Class Centers in Millimeters																										No.	Mean	Coef. Var.	M_{1913}–M_{1912}
	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59				
P_1, 1912																			1	3	4	3	3				14	54.29±.22	2.25±.29	
1913																1		3	4	7	14	30	30	11	1		101	54.97±.10	2.83±.13	+0.68±.24
P_2, 1912																1	3	2	2	2	3	2					15	52.20±.33	3.65±.45	
1913												1	1		1	2	5	3	5	7	13	53	46	29	7		173	55.05±.11	3.87±.14	+2.85±.35
P_3, 1912																1		3	1	3	3	2	1				14	52.93±.34	3.53±.45	
1913															1	1		3	3	10	12	41	20	9	2		102	54.78±.11	3.03±.14	+1.85±.36
P_4, 1912																			1	2	2	5	4	1			15	54.80±.23	2.42±.30	
1913															1	1	4	1	4	6	18	50	45	36	5		171	55.31±.09	3.08±.11	+0.51±.25
P_5, 1912																1		3	1	2	5		3				15	53.20±.35	3.77±.46	
1913																	2	3	7	17	38	42	32	7			148	54.53±.08	2.59±.10	+1.33±.36
P_6, 1912																3		3	5	1	3						15	51.67±.29	3.21±.40	
1913				2		1		1			1	5	3	6	7	11	9	11	13	19	23	39	32	12	2		197	52.75±.18	7.15±.24	+1.08±.34
P_8, 1912																1		1	6	3	4						15	52.47±.23	2.50±.31	
1913																1			1	4	9	22	25	31	17	2	112	56.07±.10	2.80±.13	+3.60±.25
P_9, 1912																			1	4	4	5		1			15	54.13±.21	2.22±.27	
1913													1		1		1		3	2	16	30	18	2	2		76	54.71±.14	3.27±.18	+0.58±.25
P_{10}, 1912																			4		5	4	2				15	54.00±.24	2.53±.31	
1913																		1	1	1	4	15	24	8	6	2	62	55.85±.12	2.59±.16	+1.85±.27
P_{11}, 1912																1	1	5	2	1	2	3					15	52.27±.33	3.59±.44	
1913															1	1	4	2	2	8	9	25	28	12	1		93	54.82±.14	3.58±.18	+2.55±.36
P_{13}, 1912																2	1	2	1	4	4	1					15	52.33±.32	3.54±.44	
1913																					3	21	32	18	12		86	56.17±.08	1.89±.10	+3.84±.33
P_{14}, 1912															1		1	2	1	2	4	4					15	52.93±.36	3.87±.48	
1913																	1	1		5	9	26	35	19	4	2	102	55.64±.10	2.56±.12	+2.71±.37
P_{15}, 1912																1				3	5	3	2		1		15	54.20±.33	3.51±.43	
1913											1		1				1	1	2	7	13	10	10	6	2		54	54.37±.23	4.57±.30	+0.17±.40
P_{16}, 1912																	2	2	4	3	4						15	52.33±.24	2.58±.32	
1913													1		2		1	4	5	10	16	30	29	10	5		113	54.73±.13	3.75±.17	+2.40±.27
P_{17}, 1912																1	4	3	5	2							15	51.20±.20	2.28±.28	
1913																1	2	1	2	10	17	34	39	17	4		127	55.17±.09	2.86±.12	+3.97±.22
P_{18}, 1912																1	3	2	5	2	2						15	51.67±.25	2.80±.34	
1913													1			3	3	2	3	13	27	30	19	2			103	54.14±.12	3.42±.16	+2.47±.28
P_{19}, 1912																	2	1	2	6	2	2					15	52.73±.26	2.81±.35	
1913	1	1		3	2	1	1	1	1	1	2	3	1	3	4	2	2	4	7	7	9	19	14	6	1		96	51.20±.41	11.52±.56	−1.53±.49
P_{20}, 1912																		1			7	1	6				15	54.67±.24	2.47±.30	
1913												1					1	2	1	8	13	25	27	23	6	1	108	55.37±.12	3.41±.16	+0.70±.27
P_{21}, 1912																	2	3	6	2	2						15	51.93±.21	2.28±.28	
1913															1		4		2	5	3	7	2	1			25	53.32±.30	4.20±.40	+1.39±.37
P_{22}, 1912																		1		5	7	2					15	53.60±.17	1.78±.22	
1913														4	1	2	2	2	11	10	17	20	23	15	6		113	54.40±.16	4.61±.21	+0.80±.23
P_{23}, 1912																		2		8	3	1	1				15	53.27±.22	2.32±.29	
1913									1				4	2	1	3	4	7	3	4	6	11	5	2	1		54	52.24±.32	6.64±.43	−1.03±.39

TABLE IX*a*

Frequency Distributions for Spread of Corollas in Individual Plants in F_1 II_{44}

Plant No.	Class Centers in Millimeters																												No.	Mean	Coef. Var.	M_{1913}–M_{1912}
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49				
P_2, 1912													7	4	3	1	2												17	35.24±.22	3.84±.44	
1913									1	1	1	1	3	2	1	1	6	10	15	13	24	27	12	14	6	2			140	41.56±.18	7.55±.30	+ 6.32±.28
P_3, 1912					1	5	5	2	1	1																			15	28.00±.22	4.52±.56	
1913							2				1	2	4	3	6	7	20	21	21	15	11	3	2	1					119	38.89±.17	7.17±.31	+10.89±.28
P_5, 1912						1	3	3	4	2	2																		15	29.60±.25	4.91±.60	
1913														1	1	7	4	12	20	28	29	26	16	4	4	1			153	41.50±.12	5.21±.20	+11.90±.28
P_7, 1912												2	7	3	3														15	34.47±.18	2.97±.37	
1913															2	3	1	6	17	19	30	39	36	30	21	12	1	1	218	43.17±.11	5.38±.17	+ 8.70±.21
P_9, 1912										1	1	2	3	3	4	1													15	34.47±.28	4.72±.58	
1913													1	1	4	9	15	23	45	37	38	18	14	2					207	40.61±.09	4.96±.16	+ 6.14±.29
P_{10}, 1912										1	2	4	3	3	2														15	33.73±.25	4.26±.52	
1913							1				1	2			2	5	11	18	30	24	18	5	1						118	39.85±.14	5.66±.25	+ 6.12±.29
P_{11}, 1912									1	3	5	1	2	3															15	32.60±.28	4.86±.60	
1913		1		3		2	3	1	5	7	13	18	19	23	27	24	24	12	13	6		1							202	35.36±.16	9.51±.32	+ 2.76±.32
P_{12}, 1912											1	3	4	4	2	1													15	34.40±.23	3.80±.47	
1913				1												2	1	2	4	8	7	10	20	16	24	20	6	5	126	44.48±.19	6.95±.30	+10.08±.30
P_{13}, 1912												1	4	2	2	3	3												15	35.73±.29	4.62±.57	
1913													1		1	1		4	10	15	22	32	37	23	13	2	1		162	43.09±.11	4.84±.18	+ 7.36±.31
P_{14}, 1912									2	1	3	3	4	1	1														15	32.87±.29	5.08±.62	
1913									1				1		3	7	9	30	38	30	28	19	10		1				177	40.52±.11	5.16±.19	+ 7.65±.31
P_{15}, 1912								3	5		2	2	2	1															15	31.33±.35	6.35±.78	
1913												1				4	7	20	10	17	24	26	25	18	3	1			156	41.96±.13	5.70±.22	+10.63±.37
P_{17}, 1912												1	4	5	3	1	1												15	35.13±.22	3.58±.44	
1913				2		2	1	1	9	1	14	14	23	29	33	57	48	41	54	33	11	4	4						381	37.30±.11	8.52±.21	+ 2.17±.25
P_{18}, 1912													1	2	3	4	2		3										15	37.07±.31	4.87±.60	
1913				1	1		1	1				2	6	7	9	6	9	10	15	13	19	23	14	23	14	10	4		188	41.37±.21	10.29±.36	+ 4.30±.36
P_{19}, 1912						3	1	2	4	4	1																		15	29.53±.28	5.37±.66	
1913		2	2	2	5	6	8	8	4	12	21	19	27	20	15	8	9	2	1										171	32.73±.18	10.68±.39	+ 3.20±.33
P_{20}, 1912					1	4	5	2	2		1																		15	28.27±.26	5.24±.65	
1913				2		3	2	5	15	14	20	22	35	36	33	37	23	13	14	6	2								282	34.96±.13	9.06±.26	+ 6.69±.29
P_{22}, 1912															2	2	3	1	2	1	1	2	1						15	39.47±.44	6.47±.80	
1913											1	2		1	5	5	6	4	14	12	27	17	21	21	16	7	4	3	166	42.60±.17	7.66±.28	+ 3.13±.47
P_{23}, 1912									2	3	5	2	2	1															15	32.13±.25	4.38±.54	
1913													2	1	7	4	12	14	9	2									51	38.18±.16	4.33±.29	+ 6.05±.30
P_{24}, 1912						1	1	3	3	3	1	1	1	1															15	30.60±.37	6.94±.85	
1913	2	2	3	3		3	6	6	12	8	10	9	10	16	14	16	11	3	2										136	33.06±.24	12.49±.51	+ 2.46±.44
P_{25}, 1912										1	1	2	3	3	3	2													15	34.53±.40	4.95±.61	
1913													1	8	4	14	26	25	17	3	3								101	38.30±.11	4.33±.21	+ 3.77±.41

TABLE IX*b*

Frequency Distributions for Length of Corolla in Individual Plants in F_1 H_{44}

Plant No.	Class Centers in Millimeters																														No.	Mean	Coef. Var.	$M_{1913}-M_{1912}$
	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63				
P$_2$, 1912																		1	1	3	4	6	2								17	54.12±.22	2.45±.28	
1913													1			1	2	1	6	15	32	42	19	17	4						140	54.69±.10	3.23±.13	+0.57±.24
P$_3$, 1912																			3	1	3	3		5							15	54.73±.33	3.43±.42	
1913			1			1				1			1	2	2	2	4	3	12	19	24	21	16	6	2	2					119	53.44±.20	6.17±.27	−1.29±.38
P$_5$, 1912																			1		3	2	6	2	1						15	55.47±.25	2.62±.32	
1913																2	9	1	9	12	23	29	33	20	10	5					153	54.92±.12	4.02±.16	−0.55±.28
P$_7$, 1912																1	5	6	3												15	50.73±.18	1.52±.19	
1913								1								3	2	26	40	58	55	27	6								218	53.02±.08	3.12±.10	+2.29±.20
P$_9$, 1912																	1	1	1	3	4	2	3								15	53.73±.30	3.22±.40	
1913														1	1	1		1	4	5	17	48	66	39	22	2					207	55.74±.08	2.99±.10	+2.01±.31
P$_{10}$, 1912																		1	1	3	7	2	1								15	53.73±.21	2.20±.27	
1913												1			2		1	3	4	9	12	34	36	12	4						118	54.91±.12	3.65±.16	+1.18±.24
P$_{11}$, 1912																						1	2		2	2	2	4	1	1	15	59.33±.40	3.83±.47	
1913								1				4	2	2	4	4	5	6	13	10	10	17	19	26	15	22	25	11	6		202	55.89±.19	7.32±.24	−3.44±.44
P$_{12}$, 1912																					2	3	7	3							15	55.73±.16	1.67±.21	
1913						1							1		1	2	1	2	1	11	6	21	31	23	21	3	1				126	55.55±.16	4.87±.21	−0.18±.23
P$_{13}$, 1912																	2	1	4	7	1										15	52.27±.20	2.15±.26	
1913											1				3	5	12	22	48	37	27	6	1								162	52.20±.09	3.14±.12	−0.07±.22
P$_{14}$, 1912															2		2		5	4	1	1									15	51.80±.34	3.74±.46	
1913									1				1	1	3		9	19	22	27	56	20	17	1							177	53.14±.11	3.90±.14	+1.34±.36
P$_{15}$, 1912																				3	5	3	4								15	54.53±.19	1.99±.25	
1913																5	3	7	8	22	46	37	19	3	4	1		1			156	54.10±.10	3.52±.13	−0.43±.21
P$_{17}$, 1912														1	5		5	4													15	49.40±.29	3.49±.42	
1913		1				1	2	7	3	8	14	14	15	24	41	33	60	64	48	27	16	3									381	49.29±.11	6.45±.16	−0.11±.31
P$_{18}$, 1912																2	2	3	1	3	3		1								15	52.00±.35	3.85±.47	
1913	1				1	1	1	3	2	2		4	3	7	9	12	19	9	18	15	8	9	18	22	17	6		1			188	52.35±.24	9.14±.32	+0.35±.42
P$_{19}$, 1912												4	6	2	3																15	46.27±.19	2.30±.28	
1913			2	1	1		2	6	10	7	12	13	9	11	7	17	34	17	16	4	2										171	47.52±.20	8.07±.29	+1.25±.28
P$_{20}$, 1912													1				1	1	4	4	3	1									15	52.27±.36	3.98±.49	
1913					1	1	1	1		2	3	9	10	8	6	10	11	23	13	27	17	37	37	28	20	10	7				282	53.25±.17	8.05±.23	+0.98±.40
P$_{22}$, 1912																		2	6	1	2	4									15	53.00±.25	2.76±.34	
1913													1	1	4	1		3	4	6	9	35	43	25	23	10	1				166	55.67±.13	4.31±.16	+2.67±.28
P$_{23}$, 1912							1							3	3	7		2													15	48.67±.21	2.45±.30	
1913															1	2	2	4	5	11	14	10	1	1							51	53.18±.17	3.47±.23	+4.51±.27
P$_{24}$, 1912														2		3	1	6	2	1											15	50.27±.29	3.37±.41	
1913	1					2	3	4	2	1	1	6	6	7	8	8	7	15	13	25	12	9	4	2							136	50.11±.25	8.76±.36	−0.16±.38
P$_{25}$, 1912																	3	3	2	3	3	1									15	52.20±.28	3.07±.38	
1913																			1	4	17	23	31	19	5	1					101	55.59±.09	2.36±.11	+3.39±.29

with the number taken in 1913. The first set of measurements was, however, taken with unusual care, since it was in both cases desired to measure all the plants on the same day, and since it was recognized at the time that to do so only a few measurements could be taken. When the measurements were made the terminal inflorescences were practically out of flower and only the largest flowers and those shedding pollen, on the flowering laterals were measured. The method of taking measurements in 1913 has already been described.

In Tables VIII*a*, VIII*b*, IX*a*, and IX*b* are given the distribution for individual plants of F_1 H_{38} and F_1 H_{44} in 1912 and the same plants cut back and flowering in 1913. In the last column is given the differences between the means and the probable errors of these differences.

As a third consideration under the general heading "age of plant factor," we have data bearing on the influence on flower size of the presence of developing seed capsules following the earlier flowers of the plant. In the earlier experiments on the inheritance of flower size in Nicotiana (cf. Goodpseed, 1912) the effort was made to measure every fully developed flower each day on all the plants under consideration. In such a case there are at the end of the period of measurement no developing or matured seed capsules on the plant. It was early observed that when these plants, from which all the flowers had been picked off for a month or more, were allowed to make seed normally the flowers they bore among the developing seed capsules were distinctly smaller than those previously measured. When this particular point was investigated in 1913, the observations previously made were strikingly confirmed and the distinct relation between the longevity of the plant and the amount of seed allowed to mature was further evidenced.

Figures 1 and 2 bear out the above statement without room for doubt or question. Figure 1 shows two plants of 13 22/07; Plant 14 on the right and Plant 15 on the left in the photograph. The photograph was taken 2 weeks after the last measurement on Plant 15. In the case of Plant 15 the flowers too old to be measured and developing seed capsules were picked off twice a week, while from Plant 14 only the 42 flowers measured were removed. Every fully developed flower present on Plant 15 on each of the dates of measurement was measured. In a month the spread of corolla of flowers on Plant 14 dropped from 27.38 mm. to 21.60 mm., or 5.78 mm., while during a similar period the spread of flowers on Plant 15 had decreased in size only 0.75 mm. Nearly a month later the corolla spread of Plant 15 had decreased 2.29 mm. while on Plant 1, which also was measured on September 22, the decrease in spread was 5.40 mm. A somewhat corresponding situation holds for the length of corolla. Thus on Plant 14 the decrease in length was 4.55 mm. and on Plant 15 it was only 0.25 mm. Nearly a month later the decrease in the case of Plant 15 was 0.79 mm. and that of Plant 1 was 4.00 mm. Plant 15 continued to flower until the middle of December by which time the other 74 plants of 13 22/07 had been dead for over two months.

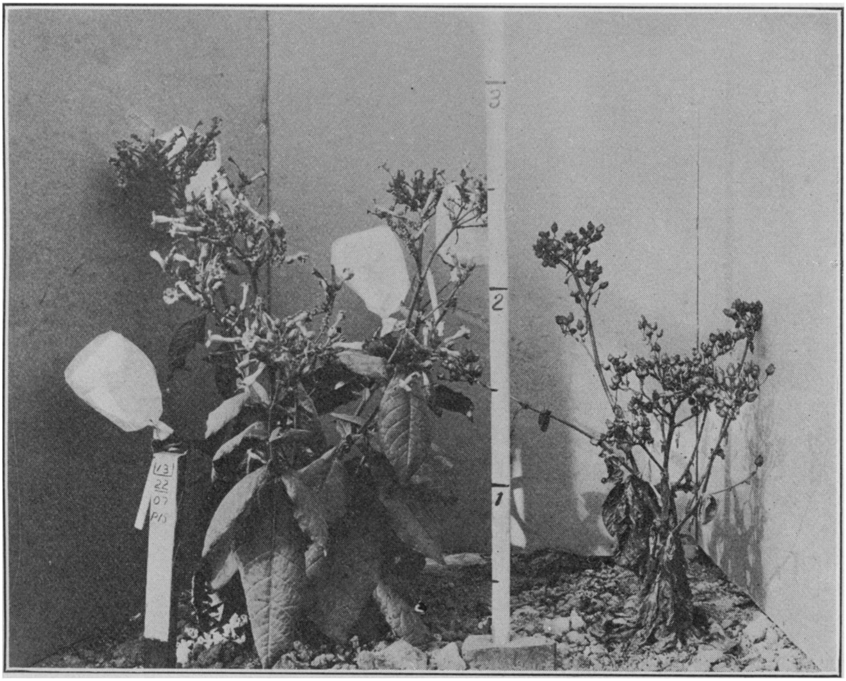

FIG. 1. Influence of removal of flowers on plants 13 22/07.

Figure 2 represents two F_2 plants of H_{103} which is a hybrid between two flower size varieties of *N. acuminata* (cf. Goodspeed, 1912). Tables X*a* and X*b* give the distribution of spread and length of corolla for Plants 13 and 14 of this hybrid, 13 F_2 H_{103} P_2. As will be seen these

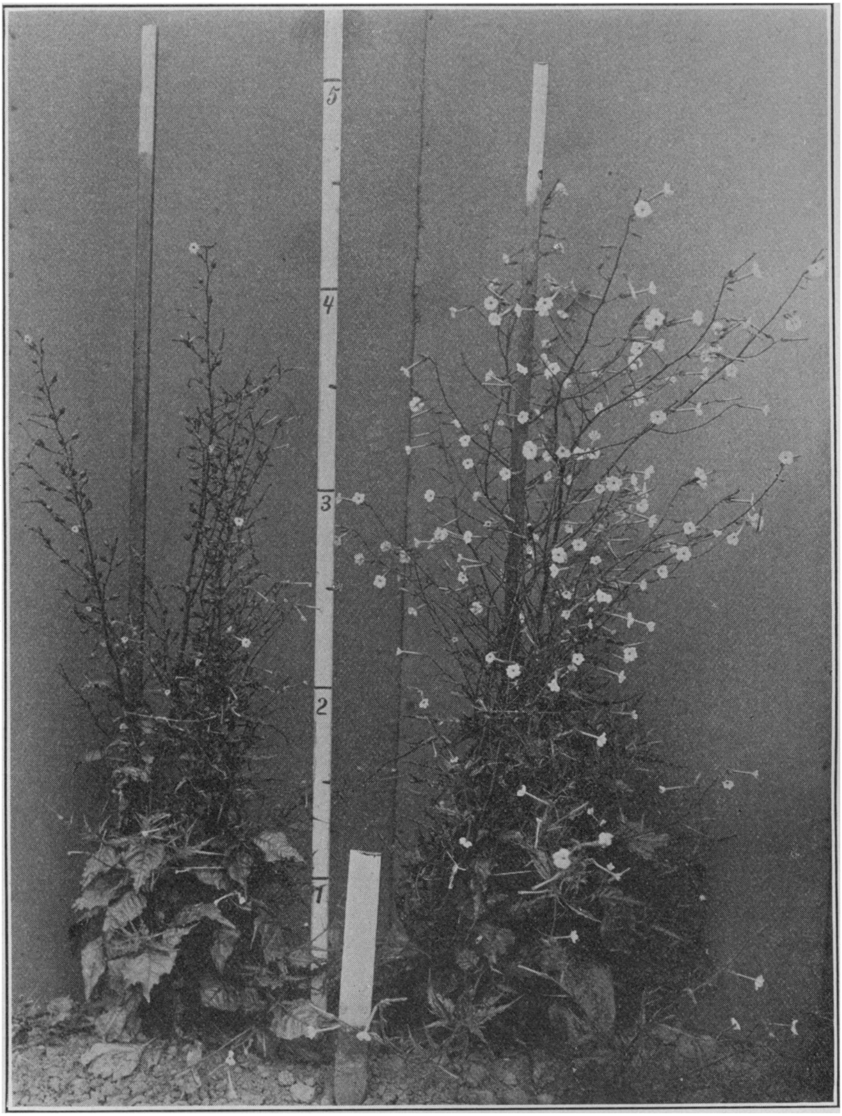

FIG. 2. Influence of removal of flowers on plants 13 $F_2H_{103}P_2$.

F_2 individuals were practically identical in spread and length of corolla on the first dates of measurement. They may, therefore, be compared with each other directly, so far as flower size is concerned. In the case of Plant 13, the old flowers and developing seed capsules were picked off, while Plant 14 was allowed to mature seed normally and only the 49 flowers measured were removed. The difference between the size of the few flowers present on Plant 14 and the numerous flowers on Plant 13, as seen in figure 2, is striking. Table X*a* shows that for spread of corolla in Plant 13 the decrease in size during the period of measurement was only 0.15 mm. as contrasted with a decrease of 6.50 mm. for the flowers of Plant 14. Similarly for length of corolla, Plant 13 showed a decrease of 1.16 mm. while Plant 14 showed a decrease of 5.17 mm.

TABLE X*a*

Influence of Removal of Flowers on Spread of Corolla in 13 F_2 H_{103} P_2

Plant No.	Date	Class Centers in Millimeters													No.	Mean
		14	15	16	17	18	19	20	21	22	23	24	25	26		
P_{13}....	August 22.....									3	4	3	2		13	23.23
	August 25.....							1		3	5	1	2		12	22.92
	September 9...				1	1		1	1	3	3	1		1	12	21.75
	September 20..							1	2	2	1	3	2	1	12	23.08
P_{14}....	August 22.....								1	2	3	2	2	2	12	23.67
	August 25.....								2	2	5	3	1		13	22.92
	September 9..					2	1	2	5	1	1				12	20.42
	September 20..	1	1	1	6		3								12	17.61

TABLE X*b*

Influence of Removal of Flowers on Length of Corolla in 13 F_2 H_{103} P_2

Plant No.	Date	Class Centers in Millimeters														No.	Mean
		28	29	30	31	32	33	34	35	36	37	38	39	40	41		
P_{13}...	August 22...								1	1	2	5	1	2	1	13	38.08
	August 25...						1	1	1	3		5		1		12	36.67
	September 9.					1				4	4	2		1		12	36.67
	September 20							3		1	4	2	2			12	36.67
P_{14}...	August 22...							1	1	6	2	2				12	36.25
	August 25...								3	3	3	3		1		13	36.77
	September 9.								3		1	5	3			12	37.42
	September 20	1	1	2	4	2	1		1							12	31.08

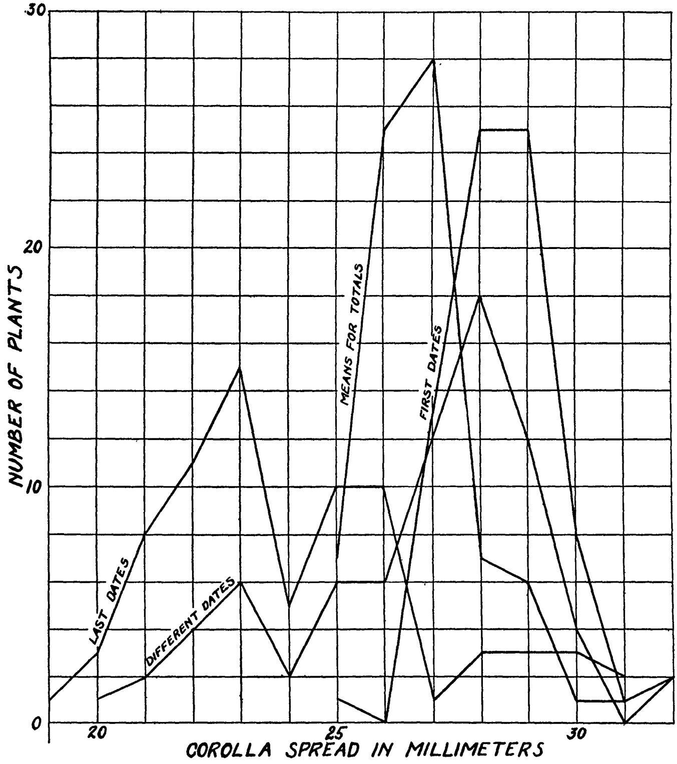

FIG. 3. Frequency polygons of variation for corolla spread of 13 22/07.

2. "*Age of Flower*" *Factor*

Under this heading, "'Age of Flower' Factor," we desire to illustrate two rather distinct sets of phenomena with reference to flower size in Nicotiana; first, the fact that at any given date throughout the flowering season the flowers on the terminal inflorescence differ in size from those borne on the laterals which come into flower late in the growing season, and second, the fact that with reference to apparently fully opened flowers, those with anthers shedding pollen are larger than flowers which are not shedding pollen. Tables XI*a*, XI*b*, XII*a*, XII*b*, XIII*a*, XIII*b*, XIV*a*, XIV*b*, XV*a*, and XV*b* illustrate these points.

TABLE XIa

Frequency Distributions for Corolla Spread of Flowers of 13(11) F_1 H_{38}

Time	Class Centers in Millimeters																				No.	Mean	Coef. Var.
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43			
Before anthesis.......	1	2	5	4	8	7	10	8	10	13	12	19	17	20	10	2	3				151	33.37±.20	11.04±.43
After anthesis........						2	3	3	6	6	15	7	12	14	34	48	52	19	3	1	225	37.90±.12	7.32±.23
Difference in means...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.....	4.53±.23	

TABLE XIb

Frequency Distribution for Tube Length of Flowers of 13(11) F_1 H_{38}

Time	Class Centers in Millimeters																		No.	Mean	Coef. Var.
	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60			
Before anthesis..........	2	2	3		5	5	2	9	4	11	6	10	18	35	23	16			151	54.01±.20	6.76±.26
After anthesis...........					1	2		5	1	18	15	13	30	53	42	29	14	2	225	55.63±.10	4.16±.13
Difference in means....	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	......	1.62±.22	

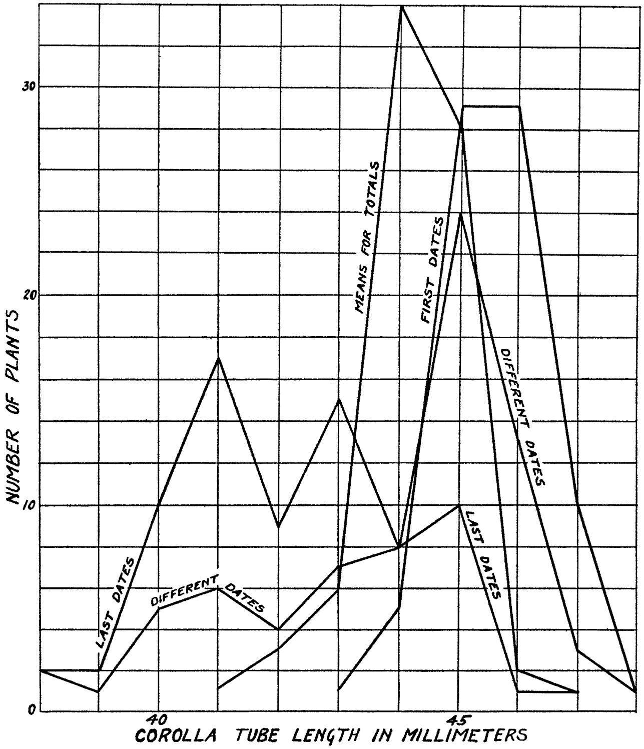

FIG. 4. Frequency polygons of variation for corolla tube length of 13 22/07.

With reference to the difference in size of fully opened flowers before and after the shedding of pollen the data is given in Tables XI*a*, XI*b*, XII*a*, and XII*b*. In these tables the flowers measured before shedding pollen, designated "before anthesis" in the tables, are compared with flowers measured on the same dates on the same plants after shedding pollen, designated "after anthesis" in the tables. In the case of 12 (11) F_1 H_{38}, the difference between the spread of "older" and "younger" flowers reaches more than 5 mm. for individual plants and averages 4.53 ± .23 mm. for the 10 plants measured. A corresponding condition does not hold for length of corolla where the maximum difference in size does not reach 3 mm. and averages only 1.62 ± .22 mm. For the "older" and "younger" flowers of 13 F_1 H_{137}, we have the same situation as shown in Tables XII*a* and XII*b*. The

TABLE XII*a*

Frequency Distribution for Corolla Spread of Flowers of 13 F_1 H_{137}

Time	Class Centers in Millimeters																	No.	Mean	Coef. Var.
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42			
Before anthesis............	1	5	5	5	13	9	21	30	22	20	14	13	4	1				163	33.13±.14	8.11±.30
After anthesis.............		3	6	13	11	16	15	14	14	24	27	66	69	58	33	14	1	384	36.31±.11	9.16±.22
Difference between means..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.....	3.18±.17	

TABLE XII*b*

Frequency Distribution for Tube Lengths of Flowers of 13 F_1 H_{137}

Time	Class Centers in Millimeters																	No.	Mean	Coef. Var.
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60			
Before anthesis............						1	2	2	2	9	14	33	46	35	19			163	55.68±.09	3.04±.11
After anthesis.............	1		1	1	3	1	6	11	15	32	28	76	104	75	27	2	1	384	55.21±.07	3.87±.09
Difference between means..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.....	.47±.11	

TABLE XIII*a*

Frequency Distribution for Corolla Spread of Flowers of 13(11) F_1 H_{38}

Position	Class Centers in Millimeters																			No.	Mean	Coef. Var.
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41			
On laterals.............							2	3	3	6	6	15	7	12	11	12	13	13	3	106	36.14±.20	8.30±.38
On terminals............	2	1		5	7	2	7	10	4	5	5	3	10	7	10	4	4	1		87	32.40±.31	13.15±.67
Difference between means	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	....	3.74±.37	

TABLE XIII*b*

Frequency Distribution for Tube Length of Flowers of 13(11) F_1 H_{38}

Position	Class Centers in Millimeters																				No.	Mean	Coef. Var.
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57			
On laterals..........										1	2		5	1	18	15	9	26	22	7	106	53.98±.14	3.92±.18
On terminals........	1			2		1	2	3	7	5	10	6	9	8	5	13	9	6			87	49.89±.26	7.27±.37
Difference between means	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	4.09±.30	

spread of the "younger" flowers averages 3.18 ± .17 mm. smaller than the spread of "older" flowers, while the length of "younger" flowers is slightly greater, .47 ± .11 mm., than that of the "older" flowers. This condition is undoubtedly due to the indirect method of comparison which we have here adopted and not to any actual shortening of the corolla tube. At the same time it renders even more significant the increase in corolla spread after anthesis which was found in measurements on the same flowers. This fact has been confirmed by direct measurements on a few individual flowers at these two stages in development. The length of time that intervenes between these two conditions in the flower is dependent to a considerable degree on weather conditions in the field, but in general occupies from 3 to 10 hours. We may, therefore, state that the spread of the flowers on these F_1 species hybrids increases distinctly within the period intervening between the opening back of the corolla limb and the dehiscence of the mature anthers, while, as might have been expected, the length of the corolla tube increases only slightly, if at all, during a corresponding period.

TABLE XIV*a*

Frequency Distribution for Corolla Spread of Flowers of 13 F_1 H_{137},

Position	Class Centers in Millimeters											No.	Mean	Coef. Var.
	31	32	33	34	35	36	37	38	39	40	41			
On laterals					1	9	14	13	17	9	2	65	38.09 ± .12	3.71 ± .22
On terminals	1	3	10	11	6	5	4	4	1			45	34.67 ± .19	5.47 ± .39
Difference between means	..	..	....	....	..	..	....	....	....	..	..	....	3.42 ± .22	

TABLE XIV*b*

Frequency Distribution for Tube Length of Flowers of 13 F_1 H_{137},

Position	Class Centers in Millimeters											No.	Mean	Coef. Var.
	47	48	49	50	51	52	53	54	55	56	57			
On laterals							4	6	20	21	14	65	55.54 ± .09	2.00 ± .12
On terminals	1	3		4	8	6	12	8	2	1		45	52.11 ± .20	3.78 ± .27
Difference between means	..	..	..	..	..	..	....		....	....	....	....	3.43 ± .22	

The second point under the "age of flower" factor is illustrated in Tables XIII*a*, XIII*b*, XIV*a*, XIV*b*, XV*a*, and XV*b*. For 13 (11) F_1 H_{38} and 13 F_1 H_{137} the flowers produced on the terminal inflorescences are distinctly smaller than those borne by the laterals which began flowering late in the growing season. As in the previous cases these tables represent comparisons made between flowers measured on the same dates on the same plants. The difference in size here holds true for both spread and length of corolla. With reference to the data on this point given, for 13 22/07 in Tables XV*a* and XV*b* another interesting fact is brought out. The differences between the size of flowers borne on different parts of the plant correspond to those of the two F_1 hybrids, but the amount of difference is considerably less and the differences for spread and length of corolla do not correspond so closely. This is explained by the fact that the 20 plants upon which the measurements were taken were practically the only ones which had not gone almost entirely out of flower. As noted in the field records at the time, the inflorescences on the laterals were covered with developing seed capsules, while the flowers measured on the terminal inflorescences were produced from adventitious buds among dry seed capsules that had dehisced. Physiological conditions within the plant operating to throw the balance of the products of metabolic activity to the production of seed rather than to the formation of new, normally large flowers, are more equally operative in the case of both the terminal inflorescences and the lateral inflorescences of 13 22/07

TABLE XV*a*

Frequency Distribution for Corolla Spread of Flowers of $13^{22}/_{07}$

Position	Class Centers in Millimeters																	No.	Mean	Coef. Var.
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			
On laterals				8	18	25	42	48	53	41	47	48	25	21	4	1	2	383	27.55±.09	9.67±.24
On terminals	1	2	4	4	17	19	26	15	12	8	7	1						116	24.99±.14	8.67±.38
Difference between means	..		..	....	.. .	....	....	....	....	...	....	....	....	..	..	..		....	2.56±.17	....

TABLE XV*b*

Frequency Distribution for Tube Length of Flowers of $13^{22}/_{07}$

Position	Class Centers in Millimeters										No.	Mean	Coef. Var.
	38	39	40	41	42	43	44	45	46	47			
On laterals		1	11	24	37	84	99	94	27	6	383	43.70±.05	3.45±.08
On terminals	3	3	9	16	30	29	19	7			116	42.46±.10	3.60±.16
Difference between means	..	....	....	....	....	....	....	....	....	..	......	1.24±.11	....

than in the case of corresponding inflorescences of the two F_1 hybrids, which have a much longer growing season and which are almost completely sterile as compared with 12 22/07.

3. *Other Factors*

Under this heading we desire to present data which have to do with the differences in size between the flowers of plants the first year in the field and flowers on cuttings of these plants flowering in 6 inch pots in the greenhouse. Tables XVI*a* and XVI*b* give a condensed statement of the results of these measurements. The cuttings were taken during October, 1912, and came into flower in the greenhouse in April, 1913. The flowers were measured for the most part during the period from April 14 to May 12, although a few flowers were measured on some of the plants on July 28. The plants were given ordinary greenhouse treatment.

These tables bring out a rather surprising situation with reference to the flower size of the cuttings as compared with that of the original plants the first and second years. While the spread of the flowers on Plant 7 in 1913 was 8.70 ± .21 mm. larger than the spread of those measured on Plant 7 in 1912, on the other hand the spread of flowers on the three cuttings of Plant 7 lay about midway between these two means, and significantly different from either as shown in the last two columns of Table XVI*a*. In other words, the spread of flowers on the plant in the field during May 1913 and on the cuttings of this plant in the greenhouse on the same dates differed to the extent of nearly 4 mm. The length of flowers as shown in Table XVI*b* behaves differently under these same conditions. The flowers on Plant 7 in 1913 averaged only 2.29 ± .15 mm. larger than those of 1912 while for the cuttings the average length of corolla was 3.71 mm. greater than in 1912. For the plant in the field and the cuttings in the greenhouse flowering during the same period the length of corolla averaged 1.42 mm. greater in favor of the cuttings. We have then with reference to corolla spread an average flower size greater in the field than on the cuttings in the greenhouse and the reverse condition, but not so marked, in the case of corolla length.

During the past two years some 100 plants of *N. sylvestris* have been grown in groups under somewhat different field conditions and under exceedingly different greenhouse conditions. Fifty plants were grown in 1914 in a rather heavily manured, somewhat shaded, and

TABLE XVI*a*

Variation in Spread of Corolla in Different Years and under Different Conditions in F_1 H_{44} P_7

Designation	Class Centers in Millimeters																	No.	Mean	Coef. Var.	M_{1912}–M_c	M_{1913}–M_c
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49					
1912	2	7	3	3														15	34.47±.18	2.97±.37		
1913				2	3	1	6	17	19	30	39	36	30	21	12	1	1	218	43.17±.11	5.38±.17		
Cutting No. 1		1	2	3	9	9	15	21	10	1	1							72	38.99±.14	4.43±.25	−4.52±.23	+4.18±.18
" " 2			1	3	6	5	8	18	4	2								47	39.04±.16	4.16±.29	−4.57±.24	+4.13±.19
" " 3				1	3	4	9	8	10	2	1							38	39.66±.17	3.89±.30	−5.19±.25	+3.51±.20

TABLE XVI*b*

Variation in Length of Corollas in Different Years and under Different Conditions in F_1 H_{44} P_7

Designation	Class Centers in Millimeters										No.	Mean	Coef. Var.	M_{1912}–M_c	M_{1913}–M_c
	49	50	51	52	53	54	55	56	57	58					
1912	1	5	6	3							15	50.73±.13	1.52±.19		
1913	3	3	26	40	58	55	27	6			218	53.02±.08	3.12±.10		
Cutting No. 1				3	13	14	24	16	2		72	54.60±.10	2.22±.12	−3.87±.16	−1.58±.13
" " 2			2	6	8	12	14	5			47	53.96±.16	2.48±.17	−3.23±.21	−0.94±.18
" " 3			1	1	3	10	14	5	3	1	38	54.76±.15	2.49±.19	−4.03±.20	−1.74±.17

moist garden plot, and an almost equal number some distance away on higher, unshaded, and unfertilized land. Eleven of these plants in the early rosette stages were transplanted with soil into pots and grown in the greenhouse. These eleven plants were treated with 3 applications of varying amounts of sodium nitrate, one pot receiving the maximum of 120 gm. and the amounts in the remaining pots decreasing in more or less regular ratio. Thus one pot received 3 gm.; one, 6 gm.; one, 10 gm.; one, 15 gm.; one, 30 gm.; one, 45 gm.; and so on.

No detailed measurements have been taken on the size of flowers on the treated plants in the greenhouse or on the plants grown under the contrasting field conditions. Inspection, actual comparison of flowers, and a few measurements, however, leave no doubt as to the relative size of flowers on the three groups of plants. The plants growing on the garden plot are in every way more vigorous and better developed as to vegetative characters than those on the exposed, unfertilized land. An off-hand inspection of the two groups of plants is convincing as to the fact that there is an increase in size of flowers more or less proportional to the increase in vegetative luxuriance. This fact is so very apparent that it scarcely needs the confirming evidence which is given by measurement and direct comparison of flowers from the two groups of plants. Spread of corolla is considerably larger in the flowers on the plants growing in the garden plot while the length of corolla is not correspondingly increased, though it, also, is greater.

With reference to the treated plants in the greenhouse the smaller amounts of nitrate scarcely serve to increase the vegetative vigor over that of the central plants. An increase in size of vegetative characters soon occurs, however, as the amount of nitrate is increased and after a certain point falls until near the maximum of application the plants are small and weak. These latter plants produce no flowers or only a few flowers that are strikingly diminutive in size as compared with the flowers on the central plants. As the amount of sodium nitrate is decreased until the optimum amount for vegetative growth is reached, the size of flowers increases distinctly, although the flowers on the treated plants that show maximum vegetative vigor are only slightly larger than those on the control plants. Such measurements as have been taken confirm the above statements. The briefest inspection of these 11 plants has served to convince observers that the flowers on the plants the vegetative growth of which has been restricted by too large applications of nitrate are smaller than the flowers of the plants that have been treated with smaller amounts.

IV. Discussion of Results

With reference to the question of the stability of the character complex, corolla size, under conditions attending development, the results of measurements of flowers on plants of Nicotiana as tabulated and discussed above seem pertinent. East (loc. cit., p. 178) illustrated his conception of the expression "conditions attending development" by mentioning the behavior of vegetative and floral characters in Nicotiana under favorable and unfavorable conditions of greenhouse culture, under poor field conditions and under field conditions at their best, and the case of cuttings versus the plants in the field from which they came. As a result of his observations, unsupported by the presentation of numerical data, East states, first, that tobacco plants growing on land where all conditions are at their best for maximum vegetative growth bear flowers of the same size as those borne by sister plants which are forced to come to maturity on land not so favorable for maximum vegetative growth. Similar observations in the case of our cultures do not confirm any such conclusion. Very large, vigorous plants growing in rather rich garden soil bear distinctly larger flowers than sister plants not so large or vigorous growing in poor soil. For example the flowers of one plant of *N. sylvestris* chosen at random from the more vigorous group averaged 43.12 mm. in spread and 84.12 mm. in length of corolla as compared with 37.40 mm. and 78.57 mm. for the average spread and length of the *most vigorous* plant among the group growing on the poorer soil. The largest flower to be found on the 50 plants of this latter group gave a spread of 42 mm. while over 20 flowers with a spread above 48 mm. were measured on only 10 plants of the former group.

In East's cultures, secondly, the flowers borne on plants in the field and on cuttings of these plants grown in small pots in the greenhouse are of the same size. The small amount of data available seems to show that rather a different condition of affairs is present in our cultures. Cuttings of a hybrid grown in pots in the greenhouse bore flowers the spread of which averaged nearly 4 mm. smaller than the spread of flowers on the plants in the field and over 1 mm. longer as to length of corolla. Cuttings of another F_1 hybrid, F_1 H_{38}, received little or no attention in the greenhouse and the average spread of their flowers was over 8 mm. smaller and the length of corolla over 2 mm. smaller than the spread and length respectively of flowers borne on plants in the field in 1912, and still smaller than the flowers of F_1 H_{38} in 1913.

With reference to the influence upon flower size of favorable and unfavorable greenhouse treatment our results are at variance with those of East. While in his cultures the size of flower did not vary under different conditions of greenhouse culture, our plants, under conditions which may be compared with good and poor greenhouse treatment, did show a distinct modification as to flower size as well as in respect to size of vegetative characters. In a series of pot experiments in which plants of *N. sylvestris* were treated with varying amounts of sodium nitrate, the plants receiving what seemed to be the optimum amount of salt produced larger flowers than the plants which received the maximum and minimum amounts of nitrate. Thus two plants which were treated with very nearly the same amounts of sodium nitrate showed an average difference in spread of about 3 mm. and about the same average difference in length. It is interesting in this connection to note that the plant treated with less nitrate produced flowers nearly 3 mm. smaller as to spread and over 2 mm. smaller as to length of corolla as compared with the flowers of plants of *N. sylvestris* grown on poorer land, and correspondingly smaller when compared with the size of flowers borne on plants grown in richer garden soil; *i. e.*, 8.12 mm. in spread and 12.28 mm. in length.

Now these variations in flower size under varying conditions attending development are a matter of common knowledge. It need only be mentioned that it is commonly recognized in horticultural practise that certain conditions of soil and treatment are conducive to the development of flowers of maximum size, and these conditions are often stated very definitely for particular plants. These facts have not escaped the attention of biometricians who have, however, for the most part concerned themselves with the discrete variations of composite flowers. Other types of flowers have, however, been considered, as for example *Ficaria ranunculoides* Moench. For this species MacLeod (1899) determined the number of stamens and the number of pistils in each of a series of flowers borne by certain plants at the beginning of the flowering season, and again in a series of flowers at the end of the season. The observations were made on the same plants (or their asexual offspring) during two successive seasons and similar results were obtained on each occasion. Although these studies were primarily concerned with correlation phenomena, the data show the same sort of differences which we have pointed out for different characters in Nicotiana. For flowers measured early in the season as reported by from these data by Weldon (1901) the mean number of stamens was 26.73 ± .15 as contrasted with a mean number late in the season of 17.86 ± .12, a difference of 8.87 ± .19, which is certainly a significant difference. Likewise an early mean number of pistils of 17.45 ± .16 decreases to 12.15 ± .12, a difference in this case of 5.30 ± .20. If we, likewise, calculate the coefficient of variability for these series we find that it increases in the case of number of stamens from 14.01 ± .41 early in the season to 18.47 ± .46 late in the season, an increase of 4.46 ± .62 per cent. Similarly for number of pistils the increase is from 22.32 ± .65 per cent to 27.88 ± .69 per cent, an increase of 5.56 ± .95. Miss Alice Lee (1902) in connection with a study of data of several series of plants of *Ficaria verna* Huds. states that "these changes while demonstrating the fact that the four series are not random samples of the same population made a the same time, are not by any means greater than the same plant in the same locality at different periods of its season or the same plant in different districts at the same period has been known to give. They are well within the limits of local environmental or seasonal changes." Although this is not quite the same character of change as the one with which we are dealing, it nevertheless seems desirable to point out the fact that wide variations in floral organs are known which can have no important genetic significance.

Our results then go to show that under the stress of external and more or less artificial conditions attending development, flower size in Nicotiana is subject to distinct and significant variations. Our principal interest in this question of the stability of the character complex, corolla size, has been centered on the effects produced by the internal, inherent, and normal ontogenetic changes that make up practically all of what we see in the development of a plant.

A varying period of vegetative development, more or less constant for a given species, precedes the appearance of the floral organs. One seems justified in assuming, at least, that the products of metabolic activity are devoted during the earliest period of development to the establishment of an adequate system of food supply at the expense of an early provision for seed production. As the plant grows older, however, the products of metabolic activity begin to be shared by both vegetative and floral organs until finally it is possible to find the vegetative characters suffering in favor of the reproductive characters. Reactions normally proceeding in one direction are forcibly reversed or perhaps reaction products are not allowed to accumulate in the usual regions and the metabolic reactions reach a point of equilibrium at a later period and in another portion of the plant. Similarly what is recognized as a periodicity in the production of flowers means the concentration of the products of metabolic activity in different regions at different times to accomplish special and individual results. That some such process must be operative is seen in the common practice on the one hand of increasing vegetative growth by the elimination of the floral organs and of restricting maximum vegetative growth to favor the early development of characters connected with the reproductive organs (cf. Cook, 1914) on the other hand. We feel that the observations tabulated on the preceding pages demonstrate the fact that under such normal, inherent conditions attending development, the size of flowers will vary to a significant extent. The first flowers produced by the vigorously growing plant are larger than those produced near the end of the flowering season when vegetative growth is at an end. An elimination of all the seed that starts to mature is effective in shifting the whole normal period of development. When the formation of seed is prevented, the normal life of the plant may be doubled and the size of the flowers it bears will remain remarkably constant throughout the entire duration of life.

In the light of these facts, the behavior of flower size in the case of the almost completely sterile F_1 hybrids dealt with in the preceding pages, is interesting and significant. These species hybrids are in general replicas on a larger scale of their *N. Tabacum* parent, but they inherit a short lived perennial habit from their *N. sylvestris* parent. Under field conditions as they exist here these F_1 hybrids reach their maximum vegetative and floral development relatively early in the growing season normal for their parents, and maintain it with only slightly diminished vigor for four or five months. There follows a rest period of from one to three months during which the plants are only feebly flowering and portions of the vegetative organs die back. With the rainy season there comes the production of new laterals and new flowers which are larger than the flowers produced toward the end of the previous period of flowering and of practically the same size as those borne at the beginning of the previous season. In other words, the flower size of plants the second year on their own roots, at the beginning of their flowering season, is the same as that of the early flowers produced the first year. This same fact is true of the succeeding year; *i. e.*, the third season of flowering. The rest period was, of course, artificially accomplished by cutting back the plants when they began to go out of flower and so show signs of dying back. These hybrids which produce no self-fertilized seed and almost no open pollinated seed show a striking diminution in size of flowers as the flowering season advances, and after a period of rest begin again to produce large flowers. As the second flowering season advances the size of the flowers again grows less. The significance of these facts in another connection has been commented upon elsewhere (Goodspeed, 1913, 1).

With reference again to the relation of the inherent and normal conditions attending development to the size of the flower, we have seen that the flower itself has a period of increase in size after opening which is sufficiently great to be of importance. A haphazard selection of flowers to be measured might give a great enough preference to flowers not fully developed to modify the significance of the mean flower size determined. The same is true for flowers produced in different parts of the plant. It has been shown that the flowers produced on an inflorescence going out of flower or covered with developing seed capsules are smaller than those on a terminal or lateral inflorescence just coming into flower.

Throughout the discussion of the tables given above, attention has been called to the difference between the behavior of corolla spread and corolla length under the influence of various conditions. This difference is sufficiently marked to leave little room for doubt that the conditions attending development do not tend to accomplish the same result with respect to the two types of measurement which together express the flower size in Nicotiana. The facts as noted may or may not be of any special significance as far as the general question of the degree of correlation between length and spread of corolla is concerned. As noted by East (loc. cit. p. 18) it is by no means uncommon to find an individual flower with a very broad corolla limb and comparatively short corolla tube"; "but one never finds inverse extremes in the same individual." Our results show, however, that there are a considerable number of individual flowers per plant which possess only a little less than the normal length of tube but a very small diameter of corolla limb. East further states (p. 182) with reference to the correlation between spread and length in an F_2 population, that "perfect coupling of certain factors together with independent combination of others may be possible; partial coupling arising from a peculiar gametic distribution may be equally possible." Our results appear to favor East's assumption of perfect coupling of certain factors with independent combination of others, and to indicate that the perfect coupling of factors may be simply due to the fact that these factors are common to length and spread of corolla.

The sum of the conclusions above drawn makes it seem possible to state definitely that flower size, although very evidently not so markedly modified by environmental conditions as height of plant, leaf size, etc., still is not a stable character complex and is subject to marked modifications under the stress of both internal and external conditions attending development. The demonstration of these facts makes necessary in the future a more detailed description of technique and general method of flower size investigations than is ordinarily included in the published reports. On general principles it would seem rather necessary in a report on flower size inheritance to mention something of the technique of taking the measurements and at least a statement as to the number considered necessary to determine a fair mean for the various individuals of the populations reported upon. The facts brought out in the preceding pages serve to show how great an influence the number of measurements taken, the period of measurement, the age of the plants, and the age of the flowers, etc., will have upon a flower size distribution.

V. Summary

In connection with the taking of some 25,000 measurements on the length and spread of corolla limb of flowers on plants of *N. Tabacum* var. *macrophylla* and three hybrids between *N. Tabacum* varieties and *N. sylvestris* the following facts were observed.

1. When the plants first come into flower the spread and length of corolla is greater than the spread and length of flowers produced on the same plants later in the growing and flowering season. This difference in size is more striking in the case of corolla spread than in the case of corolla length. Within a month or six weeks the average

spread of corolla may drop 6 mm. and the average length as much as 4.5 mm. In such a case for flowers on individual plants the difference will be greater still.

2. The F_1 *N. Tabacum* × *N. sylvestris* hybrids possess the short-lived perennial habit of *N. sylvestris* and will bloom a second and third season on their own roots. The first flowers produced the second season were of approximately the same size as the first flowers produced the first year and were considerably larger than the flowers produced toward the end of the first period of flowering. The difference in size was greater for spread of corolla than for length of corolla.

3. The removal of all open flowers during the normal flowering season will keep up the flower size to nearly that of the first flowers produced and in some cases will double the life of the plant. There is a distinct relation between the presence of developing seed on an inflorescence and the size of the flowers produced thereupon. This relation is analogous on the one hand to the agricultural practice of "topping" tobacco plants to favor vegetative luxuriance and on the other hand to the restricting of the vegetative growth in cotton to favor an earlier development of fruiting branches and thus an earlier crop.

4. Flowers that are apparently fully expanded but with the anthers unopened are smaller than fully opened flowers after anthesis. Similarly there is a striking difference in the size of flowers produced on a terminal inflorescence that is almost through flowering and on a lateral inflorescence that is just in full bloom. This difference holds for the semi-sterile F_1 hybrids as well as for the parent *N. Tabacum* var. *macrophylla* where many seed capsules are developing on the older inflorescences. Spread and length of corolla are equally diminished in size when flowers on older terminal inflorescences are compared with those on lateral inflorescences in full bloom. With reference to the difference in size of flowers before and after the dehiscence of the anthers, the spread of corolla is relatively more greatly increased after anthesis than the length.

5. The flowers on cuttings taken from plants in the field and grown in pots in the greenhouse are smaller than those borne on the plant from which the cuttings were taken. This is more strikingly evident in the case of spread than in the case of length of corolla.

6. Under favorable and unfavorable conditions of greenhouse culture flower size will vary distinctly and in the same direction as vegetative characters under such conditions.

7. The spread of corolla limb and the length of corolla tube do not behave in the same manner with reference to the operation of the various factors which are shown to be of importance in determining flower size in Nicotiana. Length of corolla is more stable than spread of corolla, which is rather readily subject to modification under the stress of internal and external conditions attending development.

8. The only true distribution representing the flower size of a population must be based upon measurements which, for each plant, extend over the greater part of the period of flowering normal for the given species or hybrid group or cover an identical portion of the flowering period of each plant. If in a large F_2 hybrid population, some plants are measured early in the flowering season, others in the middle of the flowering season, and the remainder late in the flowering season an unusually extensive range of variation in the distribution resulting may be due to modifications in flowering size dependent upon inherent ontogenetic processes and genetically of little significance.

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